Human-caused mortality triggers pack instability in gray wolves

Kira A Cassidy[1*], Bridget L Borg[2], Kaija J Klauder[2], Mathew S Sorum[3], Rebecca Thomas-Kuzilik[4], Sarah R Dewey[4], John A Stephenson[4], Daniel R Stahler[1], Thomas D Gable[5], Joseph K Bump[5], Austin T Homkes[5], Steve K Windels[6], and Douglas W Smith[1]

Transboundary movement of wildlife results in some of the most complicated and unresolved wildlife management issues across the globe. Depending on the location and managing agency, gray wolf (*Canis lupus*) management in the US ranges from preservation to limited hunting to population reduction. Most wildlife studies focus on population size and growth rate to inform management, but relatively few examine species biological processes at scales aside from that of the population. This is especially important for group-living species such as the gray wolf, for which the breeding unit is the social group. We analyzed data for gray wolf packs living primarily within several US National Park Service units (years of data): Denali National Park and Preserve (33 years), Grand Teton National Park (23 years), Voyageurs National Park (12 years), Yellowstone National Park (27 years), and Yukon-Charley Rivers National Preserve (23 years). We identified two gray wolf biological processes that differed from population size – namely, pack persistence and reproduction – and determined that while human-caused mortality had negative effects on both, pack size had a moderating effect on the impacts of mortality.

Front Ecol Environ 2023; doi:10.1002/fee.2597

Gray wolf (*Canis lupus*) management strategies in the US have ranged from eradication by any means (Musiani and Paquet 2004), to protection and recovery under the Endangered Species Act (Fritts *et al*. 1997), to state-level management, which can include predator control and hunting seasons (Ausband 2016; Schmidt *et al*. 2017; Parks *et al*. 2022; Mills 2022). This array of management approaches exemplifies long-standing human attitudes toward wolves, where management decisions have been implemented to reduce wolf–human conflict and often to align with varying levels of social tolerance toward wolves. Wolves also require extensive areas and regularly move across jurisdictional boundaries (Smith *et al*. 2016; Hebblewhite and Whittington 2020), where transboundary wildlife management issues are often complicated by conflicting managing agency goals or mandates. Most agency management objectives include target population and harvest numbers, and wildlife research has largely focused on the human impacts on these factors. Relatively few studies have examined the effects of human disturbance to biological metrics other than the population size or growth rate such as sex ratios, age structure, and social structure, yet several have reported notable impacts. For example, infanticide increased with male harvest in both African lions (*Panthera leo*) (Loveridge *et al*. 2007) and Scandinavian brown bears (*Ursus arctos*) (Leclerc *et al*. 2017), and human-caused mortality disrupted dispersal patterns in African leopards (*Panthera pardus pardus*), resulting in higher rates of inbreeding (Naude *et al*. 2020).

Gray wolves have been researched extensively and many management decisions at the state level (Horne *et al*. 2019; Mills 2022; Parks *et al*. 2022) are based on studies examining the influence of human-caused mortality on population growth rate (Fuller *et al*. 2003; Adams *et al*. 2008; Creel and Rotella 2010). However, wolf populations are composed of distinct packs, making the pack a vital unit of measure, particularly in relation to social structure and pack-level success in hunting, reproduction, disease recovery, foraging, and territoriality (Smith *et al*. 2020). Among the first to examine the impact of disturbances at the pack level, Brainerd *et al*. (2008) found that the loss of breeding wolves (hereafter, "breeders") had major implications for the rest of the pack; expanding on this work, Borg *et al*. (2015) reported that the loss of the female breeder was especially detrimental to pack maintenance. Gray wolf harvest also has impacts on demographics, such that harvest decreased recruitment beyond the number of pups directly harvested (Ausband *et al*. 2015), and survival was driven by wolf use of protected areas (Hebblewhite and Whittington 2020). Focusing on human impacts, Rutledge *et al*. (2010) found that reducing human-caused gray wolf mortality restored the natural structure of wolf packs composed of close kin, and Bryan *et al*. (2015) found that wolves in areas with heavy hunting pressure had higher levels of stress hormones. Our study focused on wolf pack-level biological processes for wolves living primarily in several US national parks.

National parks in the US are managed by the federal Department of the Interior and have a preservation mission that affords species and natural processes the highest level of protection from human impacts (Dudley 2008). The National Park Service (NPS) Organic Act lists "natural and historic

[1]Yellowstone Center for Resources, Yellowstone National Park, Yellowstone National Park, WY [*](kira_cassidy@nps.gov); [2]Denali National Park and Preserve, Denali Park, AK; [3]Yukon-Charley Rivers National Preserve, Fairbanks, AK; [4]Grand Teton National Park, Moose, WY; [5]Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St Paul, MN; [6]Voyageurs National Park, International Falls, MN

objects, and wildlife" as park resources subject to the no-impairment standard (NPS 1916). Further NPS guidance describes park resources as including "ecological, biological, and physical processes" (NPS 2011). Gray wolf biological processes are well studied but have not been officially defined for the NPS. Wolves cooperate in packs to achieve several critical milestones each year in order to persist: breeding in late winter, producing pups in early spring, and raising pups to recruitment. They also cooperate to maintain pack size, defend territory, and find prey throughout the year. Pack size and structure, territorial movements, reproduction, and pack persistence are therefore potential criteria for measuring gray wolf biological processes and determining human impacts.

We examined wolf data from five US national parks and preserves (hereafter, "parks"): Denali National Park and Preserve (DNPP, 33 years of data: 1986–2019), Grand Teton National Park (GTNP, 23 years of data: 1998–2021), Voyageurs National Park (VNP, 12 years of data: 1987–1991 and 2013–2021), Yellowstone National Park (YNP, 27 years of data: 1995–2022), and Yukon-Charley Rivers National Preserve (YCRNP, 23 years of data: 1993–2016). We report human-caused mortalities for wolves living primarily in these units, measured as the total mortalities attributed to harvest, lethal control, poaching, vehicle strikes, and capture. We determined the consequences of human-caused wolf mortalities on two measures of gray wolf biological processes – pack persistence and reproduction – and discuss the status of these biological processes as they relate to protected areas and transboundary management.

Methods

Data collection

All five of the study areas (WebFigure 1) consisted of parks within the historical and current gray wolf range in the US. Each park had a gray wolf research program and the duration and intensity of these programs varied. The parks ranged in size and extent of road access, as well as the number of land and wildlife managing agencies with which they share boundaries (WebTable 1).

Wolf monitoring effort, specific to the data needed for this study, varied little between parks. Each park used radio collaring and aerial tracking throughout the year to record pack movements, size, composition, and reproduction. Monitoring pack composition determined the presence of pups and the identities of pack breeders and leaders. Pack breeders generally are the pack leaders (formerly called alphas), and each pack usually has one male breeder and one female breeder (Mech and Boitani 2003), with the exception of packs in YNP, where subordinate breeders often occur. As a result, YNP recorded pack leaders in addition to breeders (Smith *et al.* 2020). Breeders in the other four parks were referred to as leaders in this analysis. Aerial locations were supplemented with ground observations using spotting scopes or trail cameras. Wolf pack territory configurations varied, with some occurring completely within the boundaries of the park, some occasionally traveling outside the park, and some frequently traveling beyond park boundaries.

Wolf mortalities were identified directly and when a collar emitted a mortality mode after a period of time with no movement. In some cases, mortality data were collected on uncollared wolf carcasses found by or reported to park staff. Cause of death was determined through necropsies performed by staff or by reports from hunters or other wildlife officials.

Data analysis

For wolves in the five parks, we summarized the extent of human-caused mortalities as compared to natural mortalities, and also summarized the breakdown of human-caused mortalities by specific cause: harvest, lethal control, poaching, vehicle strike, or capture (either a fatal reaction to the capture drugs or an accidental, natural death while under the effects of the capture drugs – for instance, being killed by other wolves or bison). We examined pack-years, measured from the spring count just prior to the birth of new pups to the following spring (one biological year). We calculated the proportion of packs that persisted to the end of the biological year and reproduced the spring following the focal biological year ($y+1$) for packs with zero human-caused mortalities and packs with at least one human-caused mortality. We used z-tests to assess the statistical significance between the proportion of packs that persisted and reproduced with no recorded human-caused mortalities as compared to packs with at least one recorded human-caused mortality.

To determine the effect of human-caused mortality on pack persistence and reproduction, we used generalized linear mixed models (GLMMs) with a binomial distribution via the program STATA (Stata Corporation; College Station, TX). We measured pack persistence by determining when a pack formed and dissolved, with persistence marked as Yes (1) for all years until the dissolution year, which was marked as No (0). Dissolution was defined as pack size dropping below two resident wolves. Lone wolves were not considered a pack and often roamed widely without a territory (Mech and Boitani 2003). Reproduction was documented each spring and recorded as Yes (1) based on consistent pack movements around a den or observation of at least one pup. Reproduction was recorded as No (0) if the pack did not localize and no pups were observed. If a pack did not persist to the end of the biological year (persist = 0), it could not reproduce the following year (reproduce = 0).

Pack size was determined at several points throughout the year based on aerial and ground observations or extrapolated from a prior or later count, depending on each park's seasonal monitoring effort (WebPanel 1). To account for repeated measures and for unmeasured variables, we included two random intercepts: pack name (because territory location will change the human-related hazards for certain packs more than others) and year (because wolf management outside of protected areas sometimes changed from year to year). We considered park name as a random

variable. However, after applying *z*-tests to evaluate differences between persistence and reproduction by park, we found the park name variable to be unimportant. Pack name was a more fine-scale measure of risk so we dropped the coarser variable, park name, from the models.

Previous studies have examined if human-caused mortalities in gray wolf populations are additive or compensatory (Creel and Rotella 2010; Murray *et al.* 2010). In our study, we examined human-caused mortalities at the pack level only. Packs with no human-caused mortalities likely experienced natural mortalities, and packs with different levels of human-caused mortality experienced either similar (additive) or different levels of natural mortality (compensatory). Additive or compensatory mortality are both possible, but the interaction between these two mortality factors is beyond the scope of this study.

We compared several GLMMs using an information-theoretic approach (Burnham and Anderson 2004) with (1) a NULL model (persistence or reproduction best explained by random intercepts only) and (2) a univariate model of PACKSIZE. Pack size is important to all aspects of wolf life history (Mech and Boitani 2003; Smith *et al.* 2020), and therefore we included it in all other models: (3) PACKSIZE and TOTALMORT (all recorded human-caused mortalities in a given biological pack-year), (4) PACKSIZE and LEADERMORT (human-caused mortalities of pack leader), and (5) PACKSIZE, TOTALMORT, and LEADERMORT. On the basis of the best-performing models, we constructed fitted-value plots for the predicted probability that a wolf pack would persist and the predicted probability that a wolf pack would reproduce.

Results

Across all five parks, we monitored 193 packs over 864 pack-years and recorded 978 wolf mortalities from 1986 to 2021. On average, 5.3% of each pack died from a human-related cause each year (standard deviation [SD] = 17.2%), with no recorded human-caused mortalities in 80% of the pack-years and 1.6% of pack-years resulting in the deaths of the entire pack from human causes. The proportion of mortalities of collared wolves caused by humans ranged by park from 22 to 58% (Figure 1a) and these mortalities were

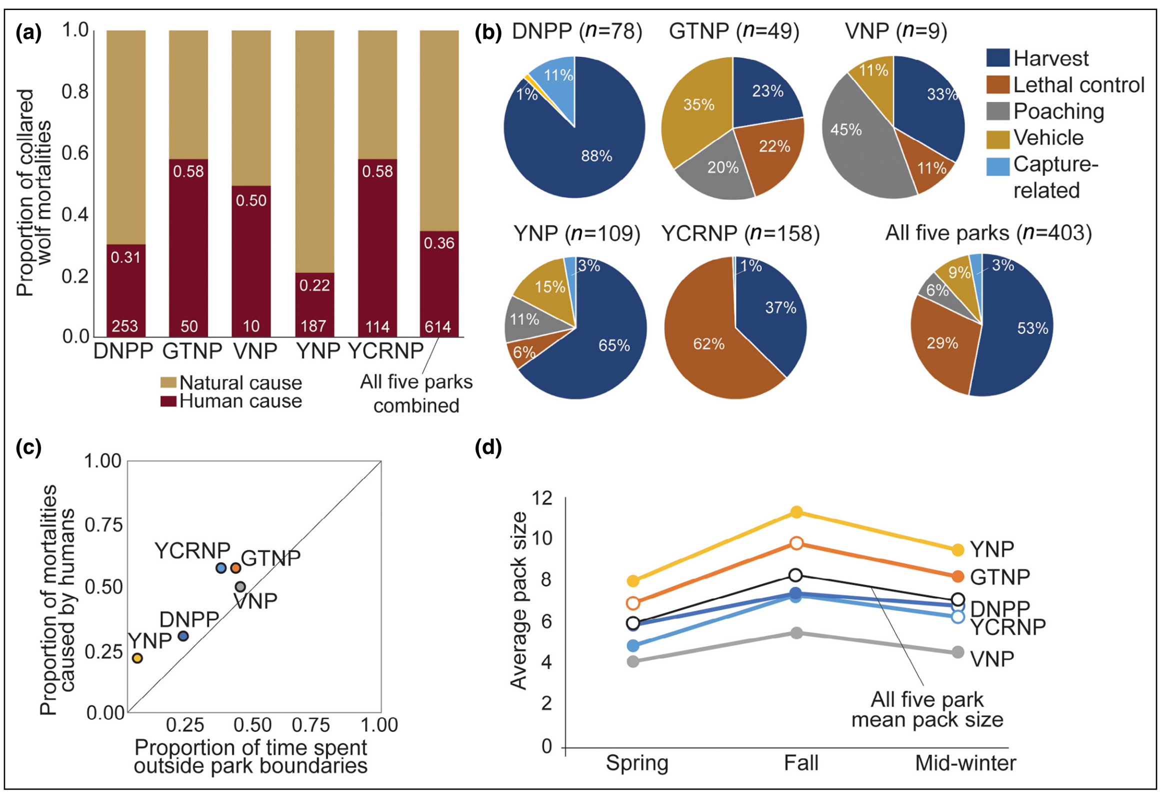

Figure 1. Gray wolf (*Canis lupus*) mortalities and pack information from 1986 to 2021 in five US national parks and preserves: Denali National Park and Preserve (DNPP), Grand Teton National Park (GTNP), Voyageurs National Park (VNP), Yellowstone National Park (YNP), and Yukon-Charley Rivers National Preserve (YCRNP). (a) Collared wolf mortalities, known-cause only, with causes of death separated into natural causes or human-caused. Total sample sizes are displayed at the bottom of each bar and the proportion of human-caused mortalities is displayed at the top of each red bar. (b) Cause-specific mortality for all human-caused mortalities (collared and uncollared wolves), with sample sizes in parentheses. Note that mortality proportions do not represent relative risk exposure. (c) Plotted points for the proportion of time that monitored wolves spent outside park boundaries by the proportion of collared wolf mortalities attributed to human-caused causes, with a 1:1 reference line. (d) Average pack size at three times of the year for each park: spring before pups are born, fall prior to most hunting and trapping seasons, and mid-winter. Solid circles indicate an official count performed by each park; in instances where pack size was not officially measured, estimates were calculated (open circles) (WebPanel 1).

categorized into five specific causes (Figure 1b). The proportion of human-caused mortalities was higher than the proportion of time wolves spent outside park boundaries (Figure 1c). Average pack size also varied between parks (Figure 1d).

Packs with no reported human-caused mortalities persisted to the end of the biological year 91.6% of the time, while packs that experienced at least one reported human-caused mortality persisted 76.3% of the time (z-score = 5.602, $P < 0.0001$) (Figure 2a). Packs with no reported human-caused mortalities reproduced the following year 79.0% of the time, whereas packs with at least one reported human-caused mortality reproduced the following year only 65.6% of the time (z-score = 3.540, $P < 0.001$) (Figure 2b).

Persistence model results

The best-performing model for determining pack persistence (WebTables 2 and 3) included pack size, total human-caused mortalities, and human-caused mortality of a leader (AICc weight [w_i] = 0.97, where AICc is Akaike's Information Criterion corrected for sample size). Pack size in the fall (coefficient estimate [β] = 0.229, 95% confidence interval [CI]: 0.159 to 0.300) was an important factor, and persistence increased with pack size. Pack persistence decreased with increasing human-caused mortalities (β = –0.309, 95% CI: –0.589 to –0.030). Packs with at least one human-caused mortality had a 27% lower likelihood of persisting (odds ratio 0.73 = exp[–0.309]). The human-caused mortality of a leader (β = –1.239, 95% CI: –1.931 to –0.548) had an even greater effect on pack persistence, causing a 71% lower likelihood of persisting.

We used the best-performing model to predict persistence based on pack size and human-caused total and leader mortalities (Figure 3a). Among packs that had no human-caused mortalities, persistence was initially moderately high for the smallest packs (0.79 for a pair of wolves) and increased to >0.90 for packs larger than six members. A pack of eight (average fall pack size for all parks combined) was very likely to persist (probability: 0.94) with no mortalities, but became less likely to persist with each additional mortality (five mortalities = 0.76 persistence probability). The effect was stronger if the human-caused mortality was a leader (one leader = 0.76, two leaders = 0.38).

Reproduction model results

The best-performing model for determining reproduction (WebTables 4 and 5) included pack size, total human-caused mortalities, and human-caused mortality of a leader (w_i = 0.94). Pack size (β = 0.173, 95% CI: 0.129 to 0.217) indicated larger packs were more likely to reproduce than small packs. Any human-caused mortality (β = –0.254, 95% CI: –0.484 to –0.024) and human-caused mortality of a leader (β = –0.674, 95% CI: –1.282 to –0.066) were also important variables, with a leader mortality having a greater effect than that of any mortality (49% versus 22% lower likelihood of reproducing, respectively).

We used the best-performing model to predict reproduction based on pack size, total human-caused mortalities, and human-caused leader mortalities (Figure 3b). The probability of reproduction for a pack with no human-caused mortalities started at 0.59 for wolf pairs and increased to >0.90 at pack sizes over 13. For a pack of eight with no human-caused mortalities, the predicted probability of reproducing was 0.8 and fell by 0.04 to 0.07 with each additional total mortality. The mortality of one leader or two leaders from a pack of eight decreased the probability of reproducing to 0.61 and 0.37, respectively.

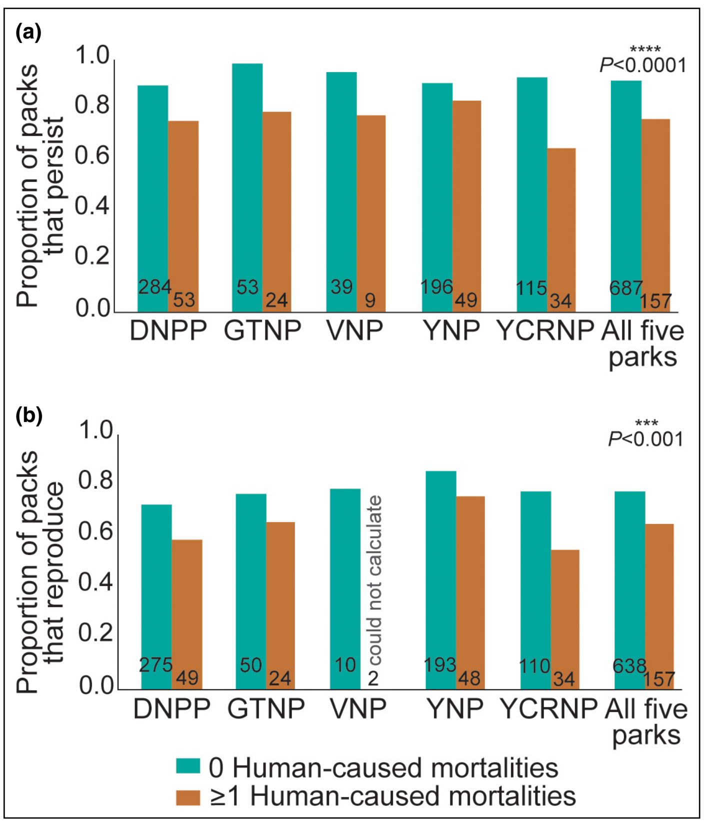

Figure 2. Proportion of gray wolf packs without human-caused mortality (green bars) and with one or more recorded human-caused mortalities (orange bars) that (a) persisted to the end of the biological year and (b) reproduced after the biological year, in five US national parks and preserves. Pack-years are indicated at the bottom of the bars and *P* values for the *z*-scores are shown above the bars for all five parks and preserves combined.

Discussion

In this study, we quantified the extent and impact of human-caused mortality on two gray wolf biological processes – pack persistence and reproduction – in five US national parks and preserves. Human-caused mortality accounted for 36% of collared wolf mortalities and had a detrimental effect

on both pack persistence and reproduction. The human-caused mortality of any wolf decreased the predicted odds of pack persistence to the end of the biological year by 27% (1: 0.73) and reproduction the following year by 22% (1: 0.78). The human-caused mortality of a pack leader decreased the predicted odds of pack persistence to the end of the biological year by 73% (1: 0.27) and reproduction the following year by 49% (1: 0.51). These results indicate that human activities can have major negative effects on the biological processes of wildlife that use protected areas.

Many studies have focused on gray wolf population-level metrics such as population size and growth rate. Although wolves seem to be well equipped to recover from fairly high levels of human offtake (Fuller *et al.* 2003; Adams *et al.* 2008), given their short time to sexual maturity and ability to produce large litters, these measures of recovery are at the population level and can disguise disruption occurring at the pack level. The pack-level measures we examined show that even the loss of a single wolf, especially a leader, can have detrimental effects on the pack. This aligns with the findings of Brainerd *et al.* (2008) and Borg *et al.* (2015) on pack persistence and mortalities. In addition, pack instability not only could possibly lead to disruptions to wolf pack kin structure (Rutledge *et al.* 2010) or even population-level perturbation, as it does for other species (Lerch *et al.* 2018), but also is an important topic for future research. Our results also show an effect on reproduction; when combined with lower recruitment after a harvest mortality in the pack (Ausband *et al.* 2015), these results warrant future attention on this vital population and pack-level measure.

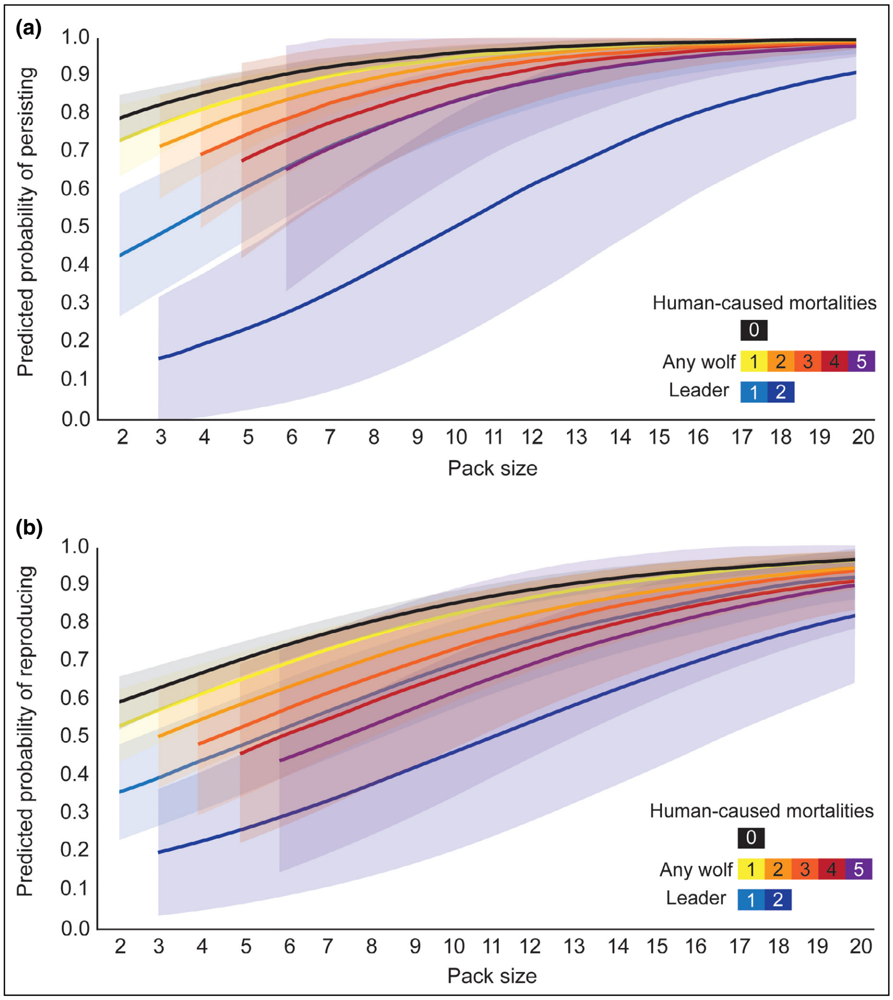

Figure 3. Predicted probabilities of a gray wolf pack (a) persisting and (b) reproducing in five US national parks and preserves based on the best-performing generalized linear mixed models.

Although pack dissolutions are natural components of gray wolf life history, our results demonstrate that these events can be influenced by human-caused mortalities. As our primary goal was to report the extent and consequence of human-caused mortality on packs, we did not examine the relationship between additive and compensatory mortality as it relates to human and natural causes at the population level. However, our results indicate that even in the unlikely case that human-caused mortality was completely compensatory, pack persistence and reproduction was still negatively impacted. This may be due to human-caused mortalities occurring at more critical times of the year for wolf biological processes, such as during the months of wolf pregnancy, or are more likely to occur in clusters (more than one wolf killed) than natural mortality. In addition, in areas with an adequate wolf population, new or neighboring packs often claim the territory of a pack that dissolves. This dynamic is evident in the differences between population-level studies, where human impacts might be minimal, and pack-level studies like this one, where human impacts can be consequential. Overall, wolf population abundance can remain stable concurrent to negative impacts on wolf social dynamics at the pack level. For wildlife managing agencies solely concerned with population-level metrics, our results showing pack-level disruption by humans may not alter policy, as population numbers may remain unchanged even with major pack turnover. However, human impacts at the pack level are of concern to agencies and organizations with goals of natural regulation and preservation of biological processes.

Pack size had a moderating effect on both pack persistence and reproduction, with larger packs better able to recover from the impacts of human-caused mortalities. Wolf pack size is critical to nearly every aspect of wolf life history, from hunting prey to raising pups to recovering from disease (Smith *et al.* 2020). Furthermore, a pack-level negative feedback loop has been found in other canids, where packs reduced to a certain size

cannot recover and eventually dissolve (Courchamp and Macdonald 2001). Human-caused mortality could have impacts beyond our focus on persistence and reproduction by reducing pack size and limiting the success or efficiency of the many biological processes dependent on pack size.

The timing and extent of transboundary movements and wolf management goals outside of national parks may reduce the sizes of packs primarily using parks, as it does for packs outside of parks (Sells *et al*. 2022). For example, recent regulations in western states (Montana and Idaho) aim to reduce wolf populations. As a result, the average harvest mortality of wolves that primarily used YNP but showed some transboundary movements, previously 4.3 per year (2009, 2011–2020), increased to at least 25 wolves (19% of the YNP wolf count) in the 2021–2022 biological year. This 480% increase contributed to the dissolution of two packs and reduced pack sizes for five of the other six packs using YNP.

Wildlife such as gray wolves and the processes and conditions that maintain them are park resources and values that are subject to the no-impairment standard (NPS 1916, 2011). Transboundary agreements between national parks and neighboring land and wildlife management agencies are critical to the management of gray wolves and ideally reflect the level of transboundary movements for each park and/or pack. We found that humans caused 22–58% of known collared wolf deaths during the 4–43% of the time wolves spent outside the parks. We recommend efforts be made to ensure that the proportion of human-caused mortalities more closely matches the proportion of time wolves spend outside park boundaries. Limiting human-caused mortalities is possible if efforts are made toward cooperative interagency goals. Specifically, jurisdictions adjacent to parks could adjust hunting seasons and lethal control near parks to accommodate cross-boundary movements and stability of packs.

In addition to interagency collaboration, parks can work within park boundaries to reduce other types of human-caused mortalities. For instance, as vehicle strikes composed 9% of human-caused mortalities, areas within parks where road mortalities are most frequent can be identified and the feasibility of implementing mitigating strategies, such as reduced speed limits or crossing structures, can be assessed. Poaching (6%) may be reduced if law enforcement is provided adequate staffing and resources and if legal consequences for poaching are severe. Parks can also help wolves maintain wild behavior, through hazing and aversive conditioning when necessary, to prevent habituation to vehicles and people, ideally without damaging wolf viewing opportunities for visitor enjoyment. These efforts should reduce human-caused mortalities by reducing wolves' susceptibility to harvest, poaching, and vehicle strikes.

Conclusion

Gray wolf management is rarely simple and transboundary wildlife issues are complicated by disparate management goals (Smith *et al*. 2016). Despite our study focusing on gray wolves that primarily lived within national parks and preserves, we documented high levels of human-caused mortality, most of which occurred outside protected-area boundaries. Of greater concern, these mortalities had detrimental effects on gray wolf pack-level biological processes. Rather than viewing this result as a failing, we hope this work encourages a renewed interest in interagency collaboration, where management of gray wolves is defined by compromise and based on science, including weighted space-use and cause-specific mortality data. If efforts are made toward this goal, these protected areas and the partners involved can serve as a model for successful transboundary issues worldwide.

Acknowledgements

Denali National Park and Preserve would like to thank L Adams, S Arthur, J Burch, D Mech, and T Meier for project leadership and data collection, as well as pilots T Cambier, S Hamilton, D Miller, R Swisher, and L Williams. Grand Teton National Park would like to thank M Jimenez, S Woodruff, and G Lust of Mountain Air Research; D Stinson, B Hawkins, K Overfield, and T Schell of Sky Aviation; M Packila of Wildlife Air; and J Pope and crew of Leading Edge. The University of Minnesota would like to acknowledge funding for this project provided by the Minnesota Environment and Natural Resources Trust Fund, as recommended by the Legislative-Citizen Commission on Minnesota Resources. Yellowstone National Park (YNP) would like to thank Living with Wolves, especially Jim and Jamie Dutcher, and G Dutcher, as well as Yellowstone Forever, A Graham and B Graham, V Gates, K Yeager and F Yeager, and the Browning family; YNP also thanks M Packila of Wildlife Air, R Stradley of Gallatin Flying Service, S Ard of Tracker Aviation, B Hawkins of Sky Aviation, J Pope and crew of Leading Edge, and T Woydziak of Baker Aviation. Yukon-Charley Rivers National Preserve would like to thank J Burch, K Joly, M Cameron, and J Pruszenski for field data collection, and pilots T Cambier, R Swisher, H McMahan, M Stott, S McMillan, G Lee, and B Niegus. All parks would like to thank the National Park Service, Living With Wolves (especially Jim Dutcher, Jamie Dutcher, and G Dutcher), and the Val A Browning Foundation. Our deepest thanks to the many field technicians, volunteers, and community members who helped us collect the data that are the foundation of this work. *Ethics statement*: All wildlife were handled in accordance with recommendations from the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016) and capture protocols were approved by NPS veterinarians (Institutional Animal Care and Use Committee numbers: DNPP: AKR_DENA_Borg_Wolves_2019.A3, GTNP: WY_GRTE_Stephenson_Wolf_2020.A3, VNP: MWR_VOYA_WINDELS_WOLF & 1905-37051A, YNP: NP_Smith_Wolf_2012.A3, YCRNP: AKR_YUCH_Sorum_Wolf_2019.A3).

Data Availability Statement

Data are available through Dryad (https://doi.org/10.5061/dryad.mkkwh713f). No novel code was used for this manuscript.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2597/suppinfo